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Changes of life-history traits and size in *Daphnia magna* during a clear-water phase in a hypertrophic lagoon (Albufera of Valencia, Spain)

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Introduction

The role of large herbivorous zooplankton, especially *Daphnia*, in promoting clear-water phases due to its grazing effect on phytoplankton is well documented (SOMMER et al. 1986, CARPENTER & KITCHNEL 1996). The PGE model of plankton succession (SOMMER et al. 1986) describes both the production of the clear-water phase (CWP) and its decline. The latter results from two main mechanisms: (1) that the herbivorous zooplankton becomes food limited due to overpopulation, and (2) that fish predation accelerates the decline of the large zooplankton species. The aim of the present study was to examine the population dynamics of *Daphnia magna* that contributed in producing a CWP in the hypereutrophic shallow lake, Albufera of Valencia. Due to the high trophic level of the lake and the drastic changes that happen during this clear-water episode, the data presented herein clearly illustrate the operation of the aforementioned mechanisms during the CWP and how they affect the size structure and life-history traits of the *D. magna* population.

Study site and methods

Albufera of Valencia (mean depth 1.2 m, area 23.2 km^2, salinity 1–2‰) is a coastal oligohaline lagoon near the town of Valencia, Spain. Details of the main limnological features have been documented by VICENTE & MIRACLE (1992). Its outflow to the Mediterranean Sea is regulated by sluicegates located in the outlet channels, according to the needs of the surrounding rice field cultivation. From November to the beginning of January, the sluicegates are closed, the rice fields remain flooded and the water level of the lagoon is about 20 cm above normal. During January and February, there is a period of higher water renewal; rice fields are emptied, water flows to the sea through the open sluicegates and the level of the lagoon drops. Rice fields remain dry until the beginning of May when they are flooded again for cultivation. During cultivation, the sluicegates are partially closed to maintain a mean water flow and a mean water level. During the 1980s, the lagoon was an '*Oscillatoria* lake' permanently dominated by populations of Oscillatoriaceae. The lake was in a permanent turbid state, with Secchi disk depth below 20 cm. At the end of the 1990s a partial diversion of sewage waters that had been flowing into it was undertaken and a slight improvement in water quality has been detected (OLTRA et al. 2001). One of the features of this improvement is the repeated occurrence, in the last years, of a CWP after the opening of the sluicegates in winter, at the end of February or the beginning of March, when the lake bottom can be seen for 10–20 days.

Samples were collected every 3 days during the CWP of 2000, at three different points (north, centre and south). Also included as a reference were the results from samples taken some time before and after this phase. Because of the similarities between the stations, the three samples from each date were treated together. Samples were taken with a 1-L plastic jar in order to have integrated water samples from the surface to the 50-cm depth. Chlorophyll *a* concentrations were evaluated spectrophotometrically, following the methods of STRICKLAND & PARSONS (1972). Zooplankton was concentrated in situ by filtering 3 L of water collected at each point with the 1-L jar, through 35-μm mesh nytal and fixed in 4% formalin. Zooplankton species were counted using an inverted microscope at 100× and 200× magnifications. The lengths of all *Daphnia magna* individuals, or at least 200 of them in the densest samples, were measured from the eye to the base of the tail spine. Males and parthenogenetic eggs and ephippia were counted separately. *D. magna* individuals were categorised into 13 size classes, with 0.2-mm intervals.

Population growth rate was calculated as $r = (\ln N_1 - \ln N_0)/(t_1 - t_0)$. The instantaneous birth date rate was calculated according to PALOHEIMO (1974) as $b = \ln(1 + E)/D$, where E is the number of

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eggs per female and D is the egg development time calculated for each sampling date mean temperature as lnD = lna + blnT + c(lnT)^2, using the coefficients given by Botrell et al. (1976). The death rate was calculated using the equation m = b – r. The size at first reproduction was determined according to Lampert (1988).

Results

In 1999, *Daphnia magna*, after its normal absence from late spring to early autumn, reappeared in the lake in November, remaining at very low densities until February 2000. Population densities of *D. magna* increased very rapidly during this month, coinciding with a conspicuous CWP, when the chlorophyll concentrations declined by one order of magnitude, from more than 200 to less than 10 µg/L (Fig. 1). During this phase rapid density fluctuations of *D. magna* could be observed with two maxima in only 11 days, reaching concentrations of up to >300 individuals/L on February 22. One month later, the population density was low again, with only 6 individuals/L. The males appeared at the beginning of the CWP but their proportions were highest towards the end of the phase. Males showed two peaks coinciding with the females, whereas ephippia were only important from the second peak of the population until the end of the CWP.

The rotifer community during the CWP also changed markedly. It was dominated by the facultative *D. magna* epibiont *Brachionus variabilis*, which developed with its carrier, but with its main peak coinciding with the first peak of *Daphnia* and its incidence thereafter being much lower. When *D. magna* reached its second and higher peak, it was an old and overcrowded population and most of its individuals were then heavily infested by *Colacium*.

The size structure of the *D. magna* population changed considerably in the CWP, always showing a large percentage of juveniles (Figs. 2 and 3). Before and after this phase the size structure was less biased towards juveniles. Furthermore, the largest size classes almost disappeared and therefore there was a decline in the numbers of eggs and ovigerous females. The number of eggs increased with the size of the

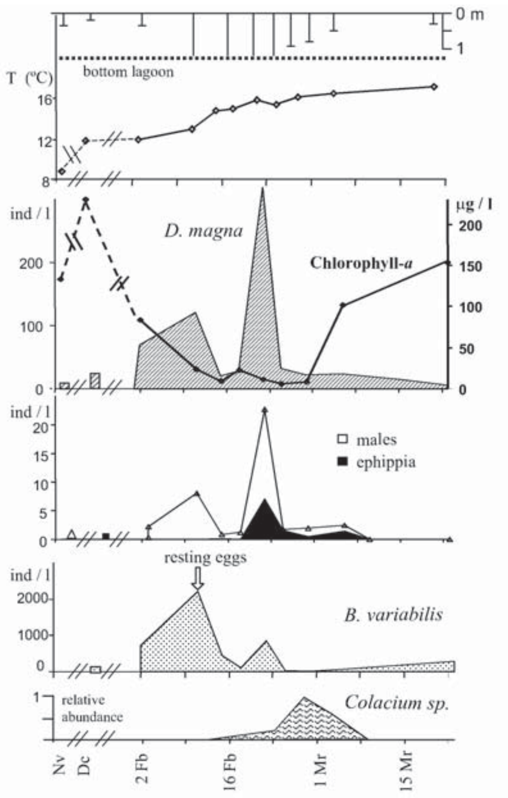

Fig. 1. Secchi disk, temperature, chlorophyll *a* and density of *D. magna* (ind./L) during and after the clear-water phase of February–March 2000. Data from samples taken on 25 November and 28 December 1999 are also included. The density of males and epphipial females of *D. magna*, as well as *B. variabilis* females, are also plotted in numbers per litre. An arrow in the *B. variabilis* graph indicates the time when a maximum of resting eggs was observed. *Colacium* density is indicated as a relative proportion with respect to the maximum infection on 29 February. All data are the means for three sampling sites.

animal; maximum sizes were found in early winter, at the same time as the largest clutch sizes. Maxima of 54 and 37 eggs, respectively, in a 3.2- and a 2.8-mm female, were observed in the December 28 samples. The most frequent clutch size was 12–18 eggs in the 2.3-mm size class on this date and at the end of March. However during the CWP, fertility decreased, more frequent clutch sizes for 2.3-mm females

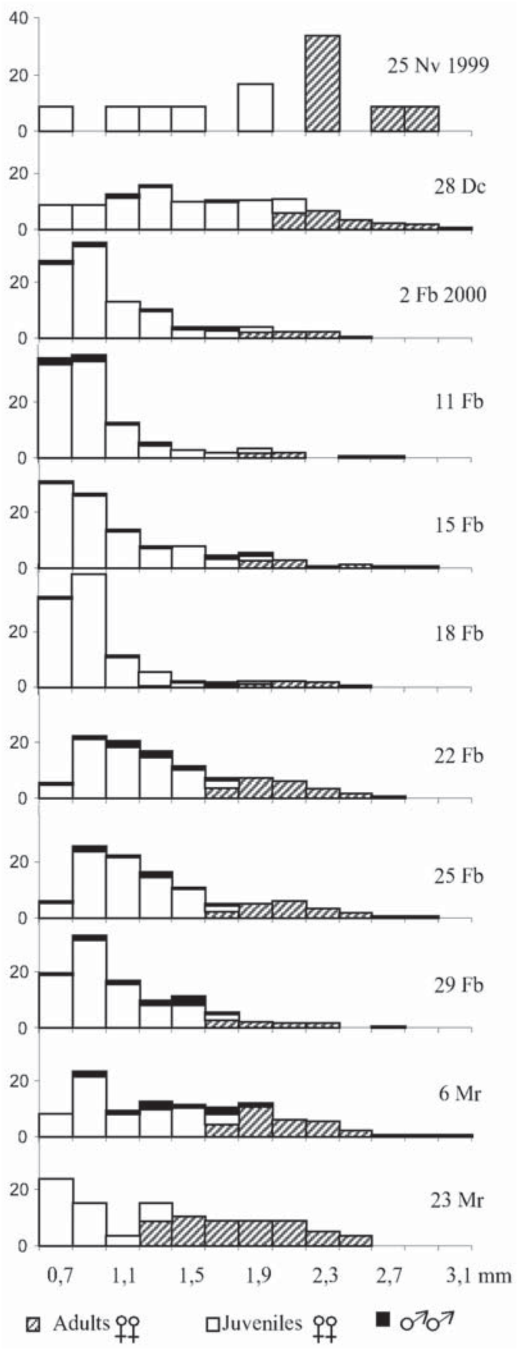

Fig. 2. Size distribution of *Daphnia magna.* Percentages of each size class (defined by its medium body size in mm) for each sampling date indicated on the right. Striped bars – adults, black bars – males.

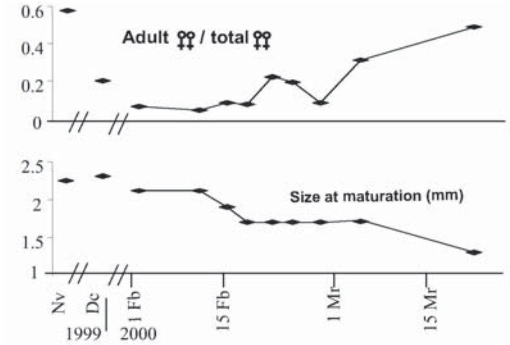

Fig. 3. Changes in the ratio of adult females to total females (top) and of the size at first reproduction (bottom) during the clear-water phase and after it. Values for the samples taken in November and December are also included (sampling dates as in Fig. 2).

were 4–11 eggs and many had no eggs. Figure 4 shows the marked decrease in the number of eggs per adult female during this period and how this was followed by an increase of ephippial females.

During the CWP the birth rate (Fig. 5) was always low, due to the mentioned scarcity of adult females and their decline in fertility. Numbers of large daphnids were extremely low during the CWP and it would seem that few *Daphnia* can reach maturity before they die or are preyed upon. The death rate (Fig. 5) then showed great fluctuations according to the wax and wane of *D. magna*. Similar results on birth and death rates were obtained in another hypereutrophic shallow lake by LAMPERT (1991), who concluded that these parameters did not well reflect the population development in that environment.

The size at first reproduction also showed a clear variation (Fig. 3). It was highest in December, slightly lower at the beginning of February and after the first peak of *D. magna* at the onset of the CWP, it diminished from 2.1 mm to 1.7 mm or less. Due to the small number of gravid adult females it was difficult to estimate the smallest size class with more than 50% of ovigerous females, at the end of the CWP, but there were sufficient animals to esti-

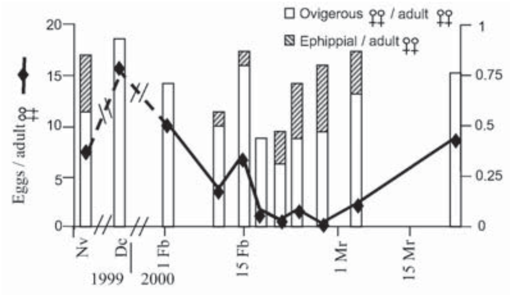

Fig. 4. Changes, during the clear-water phase and after it, of the ratios: eggs per adult female (line), ovigerous female per adult female (bars) and ephippial female per adult female (bars). Data for November and December samples are also included (sampling dates as Fig. 2).

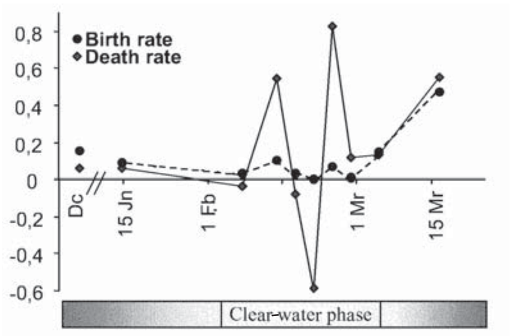

Fig. 5. Changes in birth and death rates of *D. magna* during the clear-water phase. Values are positioned in the middle of the time interval used in the calculation. Values calculated from larger time intervals in December and late March are also included.

mate it 1 month later, confirming the trend of decline, since the mean size at maturity was 1.3 mm at that time. The size of the caudal spine was also clearly variable; Fig. 6 shows that its size was relatively much larger after the CWP than before it.

Discussion

Since the partial diversion of the sewage, which improved the quality of the water coming into the Albufera of Valencia Lagoon, a conspicuous CWP is recurrently observed in winter. During January the sluicegates of the Albufera of Valencia are opened to empty the surrounding rice fields, resulting in an increase in the water flow, which dilutes the density of the dominant cyanobacterial populations and favours the development of other more edible algae (*Cyclotella meneghiniana*, Cryptophyceae, *Chlamydomonas* and other clorophyceae). The shift of phytoplankton favours the explosion of *Daphnia magna*, a cladoceran that is abundant in winter time in the entire marshland. The results show that *D. magna* then acts as an agent in favouring the change from turbid to clear water during a period of 2 or 3 weeks. Afterwards, the water becomes turbid again, indicating what other authors (Moss et al. 1998) have also concluded, that the grazing of *Daphnia* induces water clarity, but it is not a stabilizing agent of a clear-water state.

D. magna populations were sampled at close intervals when the water was already clear, thus providing more information on their decline rather than from the start of the boom. Three main factors may cause the decline: food limitation, a chemically mediated crowding effect and fish predation. Food limitation during the CWP caused the decrease in clutch size and the extraordinarily small ratios of eggs per adult female. At the same time an increase of males and ephippial females was observed due to food limitation, and most probably to a chemically mediated cue from the dense *Daphnia* populations. These two density dependent factors have been experimentally proven to be essential for sexual reproduction in *D. magna* (Kleiven et al. 1992). The high density of the daphnids (Fig. 1) also produced an increase of infestation by epibionts, first by *B. variabilis*, and after by the more invasive *Colacium*.

The lagoon contains important fish populations, mainly mullets (*Mugil cephalus*, *Liza ramada*) and carp (*Cyprinus carpio*). When the sluicegates are open in winter, juvenile mullets enter from the sea; it is evident that a concentration of daphnids such as this would attract the fish to feed on them. Fish predation is enhanced when certain abundance levels of prey are reached (Wagner & Seitz 1992) and

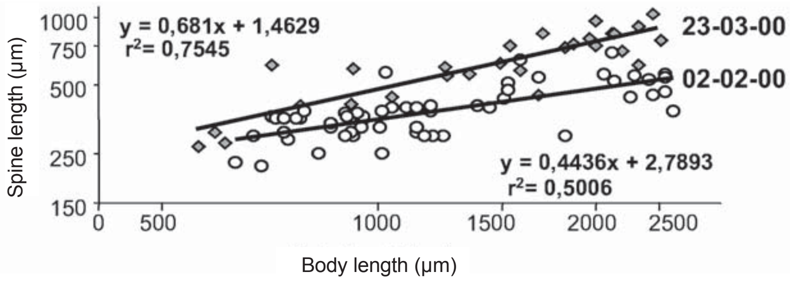

Fig. 6. A comparison of the posterior spine length in relation to body length in *D. magna,* on two sampling dates, before and after the clear-water phase.

even more if the water is clear. Mortality due to fish predation, and diminished natality due to selective predation on larger and gravid females, caused large population fluctuations in the rate of growth during the CWP. Death rates showed rapid fluctuations (Fig. 5), as in other eutrophic lakes (LAMPERT 1991). According to WAGNER & SEITZ (1992) and LAMPERT (1991), negative death rates could be explained by the hatching of resting eggs. In addition to this, another factor is that birth rates are underestimated because, when the water is not turbid, the adults seek refuge in areas close to the bottom and in the littoral, whereas the juveniles are in the open water. Although samples were taken in the water column, underestimation of the adults occurred during the first half of the CWP. However, large size classes disappeared from the plankton mainly because they were preyed upon. Also the fish in this lake are largely benthivorous and could easily find daphnids in the bottom layers. Moreover, in Fig. 2 it can be observed how the first size class diminished at the end of the CWP, having much lower proportions than the other classes, due to the aforementioned selective predation on gravid females.

The *D. magna* changes in size and form during the clear-water episode were outstanding. At the end of the CWP, size at first reproduction was extremely low (Fig. 3), and it was especially low (1.3 mm) at the beginning of spring. LAMPERT (1991) found *D. magna* sizes of 1.8–2.0 mm at maturation (measured to the top of the head) in Grosser Binnensee, indicating that they were the lowest sizes reported. Experimental studies indicate that a small size at maturity may be induced by food limitation (TILLMAN & LAMPERT 1984) and by fish predation (CERNY & BYTEL 1991). The present results indicate that, apart from a possible effect of low food conditions on the size of maturation, which were found in the CWP, as well as later, due to a decrease in edible algae, there is an important size-selective predator effect. It is clear from Figs. 2 and 3 that during the CWP there is a downward change in body size, simply due to the removal of the largest size classes by fish, and that there is also a shift of the whole size distribution due to reduced adult sizes, as an adaptive response of daphnids in avoiding fish predation. Since small-sized individuals would escape from fish but would be more easily consumed by invertebrate predators, a change in posterior spine length is associated with the reduced body size, where the spine is relatively much longer in the smaller forms, in order to be able to cope with invertebrate predation (Fig. 6). This is more apparent at the end of March when invertebrate predation is supposed to have increased. At the same time it can be observed that the birth rate (Fig. 5), as well as the proportion of juveniles (Figs. 2 and 3), are much higher in the low density *D. magna* population at the end of March. This is because fish do not easily prey on the small adults in a scarce *Daphnia* population in the now-turbid water, and because invertebrate predation pressure tends to increase the per-capita birth rate, since invertebrates consume young daphnids (POLISHCHUK 1995).

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References

Botrell, H. H., Duncan, A., Gliwicz, Z. M., Herzig, E., Hillbricht-Ilkowska, A., Kurasawa, A., Larsson, P. & Weglenska, W., 1976: A review of some problems in zooplankton production studies. – *Norw. J. Zool.* **24:** 419–456.

Carpenter, S. R. & Kitchell, J. F. (eds) 1996: *The Trophic Cascade in Lakes*. – Cambridge University Press, Cambridge, 399 pp.

Cerny, M. & Bytel J., 1991: Density and size distribution of *Daphnia* populations at different fish predation levels. – *Hydrobiologia* **225:** 199–208.

Kleiven, O. T., Larsson, P. & Hobaek, A., 1992: Sexual reproduction in *Daphnia magna* requires three stimuli. – *Oikos* **65:** 197–206.

Lampert, W., 1988: The relative importance of food limitation and predation in the seasonal cycle of two *Daphnia* species. – *Verh. Internat. Verein. Limnol* **23:** 713–718.

Lampert, W., 1991: The dynamics of *Daphnia magna* in a shallow lake. – *Verh. Internat. Verein. Limnol.* **24:** 795–798.

Moss, B., Beklioglu, M. & Kornijow, R., 1998: Differential effectiveness of nymphaeids and submerged macrophytes as refuges against fish predation for herbivorous Cladocera. – *Verh. Internat. Verein. Limnol*. **26:** 1863.

Oltra, R., Alfonso, T., Sahuquillo, M. & Miracle, M. R., 2001: Increase of rotifer diversity after sewage diversion in the hypertrophic lagoon, Albufera of Valencia, Spain. – *Hydrobiologia* **446/447:** 213–220.

Paloheimo, J. E., 1974: Calculation of instantaneous birth rate. – *Limnol. Oceanogr.* **23:** 970–988.

Polishchuk, L. V., 1995: Direct positive effect of invertebrate predators on birth rate in *Daphnia* studied with a new method of birth rate analysis. – *Limnol. Oceanogr.* **40:** 483–489.

Sommer, U., Gliwicz, M., Lampert, W. & Duncan, A., 1986: The PEG-model of seasonal succession of planktonic events in fresh waters. – *Arch. Hydrobiol.* **106:** 433–471.

Strickland, J. R. & Parsons, T. R., 1972: A practical handbook of seawater analysis. – *Bull. Fish. Res. Board Can.* 167 pp.

Tillman, U. & Lampert, W., 1984: Competitive ability of differently sized *Daphnia* species: an experimental test. – *J. Freshwater Ecol.* **2:** 311–323.

Vicente, E. & Miracle, M. R., 1992: The coastal lagoon Albufera of Valencia: an ecosystem under stress. – *Limnetica* **8:** 87–100.

Wagner, A. R. & Seitz, A., 1992: Qualitative and quantitative investigations on the cladoceran zooplankton of oligotrophic maar lakes. – *Arch. Hydrobiol. Beih*. **38:** 171–182.

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